Relationship of Sand Pine Scrub to Former Shore Lines

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No plant community in Florida has stimulated more interest and near unanimity as to its floristic distinctness and the sharpness of its boundaries with the adjacent sandhill vegetation than the Florida scrub. But much speculation has taken place as to the reasons for the floristic differences and the general lack of intergradation between these associations as well as their origins and successional relationships.

Vignoles (1823) was among the first to comment on the general similarity in the appearance of scrubs wherever found. Nash (1895) commented on the almost complete floristic difference between scrub and adjacent sandhill vegetation and stated that the "two floras are natural enemies and appear to be constantly fighting each other." He also commented, "A bare space of pure white sand usually separates the two." He considered the sands of both communities to have had the same origin and attributed the generally darker surface of the sandhill soils to be caused by charcoal deposited there by annual fires. Harper (1940) commented that fires usually sweep through the scrub about once in a lifetime. Whitney (1898) remarked that "the boundary between high pine land (sandhills) and scrub can be located without trouble within a few feet. . . . It will be shown later that there is no apparent reason, from the chemical and physical examination, to account for this difference in the native growth on the scrub as compared with high pine land—so far as our investigations show there is no difference in the soil."

Many have attributed the great vegetational differences between the communities to lower available nutrients in the scrub soils (Harper, 1921; Kurz, 1942, with reservations; Laessle 1942, 1958a). Mulvania (1931) in his study in central Florida found about 6 per cent greater water holding capacity in the sandhill soils and concluded that most of the evidence indicates that factors other than fire, such as differences in soil and water relations, account for the differences between high pine and scrub forests. Harper (1921) states that scrub soils are poor in humus, clay, and potash.

Webber (1935) considered the relatively high frequency of

fire in the sandhill community and the rarity of fire in the scrub to be the most important factor in the maintainance of the sharp boundary so generally evident when the two associations abut one another. He stated that the scrub association is a fire-fighting machine.

Both Kurz and Laessle (1942, 1958a) realized that most scrubs occupy ancient dunes formed along shore lines of higher Pleistocene sea levels, some as high as 100 feet (Kurz) or 150 feet (Laessle, 1958a) above present sea level. Kurz also pointed out that with very few exceptions the plants distinctive of scrub are also found on relatively recent coastal dunes, and some scrubs might occupy old wave formed bars or ridges.

Laessle (1958a) hypothesized that wave action along shores of lakes and even stream action could have washed and sorted sand deposits which now support scrub.

Kurz thought that the generally yellow soils occupied by sandhill vegetation would eventually be lightened in color by leaching and be succeeded by scrub vegetation. While Laessle (1942, 1958a) thought that the two communities bore no seral relationship, he also found some sandhill communities occupying typical dune sands.

Such diverse ideas on the reasons why such physionomically and taxonomically diverse communities can exist side by side with such sharp boundaries between them, often without any change of elevation from one to the other, should, I believe, be capable of a more consistent analysis and interpretation.

Methods

Vegetational changes across the ecotone between scrub and sandhill communities were studied by line transects (Buell and Cantlon, 1950). A 100 meter tape was stretched at approximate right angles to the ecotone with the 50 meter mark as close to the middle of the ecotone as could be estimated. From the zero end in the scrub, all herbs, lichens, and mosses were recorded in the order intercepted and plotted to the nearest centimeter along a line in a field notebook. On the same line the intercept to the nearest decimeter of all shrubs (here defined as woody species less than 6 feet high) and trees (woody species above 6 feet)

were also plotted. The results of six of these vegetational transects without the amount of intercept are shown as plotted from field notes for each of the three layers in Fig. 1. Some species are omitted for the sake of simplification.

Soil profiles and soil samples were taken in each community at least 20-50 meters away from the ecotone. Ten soil samples near both sides of the transect tape were taken in each community at depths of 0-2 inches, 2-6 inches, and 6-15 inches. The 10 samples from each depth were then pooled from each community and analyzed by a graduate student under the direction of Dr. Hugh Popenoe of the Soils Department of the University of Florida. Chemical analyses were made from duplicate samples after being air dried and passed through a 2 mm sieve.

Soil pH was determined using a Beckman Zeromatic pH meter with glass electrodes. One part soil to 2 parts water was allowed to stand overnight before testing in one method. In a second method KCl was added to the above solution to make a normal solution, which was stirred and allowed to stand for 30 minutes before testing. The second method is considered more accurate as it compensates for such elements as aluminum which may be present.

The exchangeable cations of Ca, Mg, Ka, and Na were extracted with normal ammonium acetate buffered at pH 4.8. Calcium and potassium were determined on a Beckman Model B Flame Spectrophotometer. Magnesium and sodium were determined on a Beckman Model DU Flame Spectrophotometer.

Extractable phosphorus was determined colorimetrically on a Baush and Lomb Spectronic 20 colorimeter using strong Bray extractant. Nitrogen was determined by titration of a boric acid solution (Kjeldahl method for total nitrogen). Organic carbon in the soil was determined by the Walkley-Black wet combustion method as modified by Walkley. Organic matter was determined using potassium dichromate as a reducing agent and titrating with ferrous ammonium sulfate (modified Walkley-Black as modified by Walkley). Mechanical analysis was done by the method of Bouyoucos (1951, 1962). The same type of analyses were made from 15 scrubs from widely scattered points as far south as Deerfield, on the lower Florida east coast and Destin in the Florida panhandle.

VEGETATIONAL TRANSECTS

Fig. 1 shows linear distribution of selected species, those that were considered most characteristic indicators of the two commu-

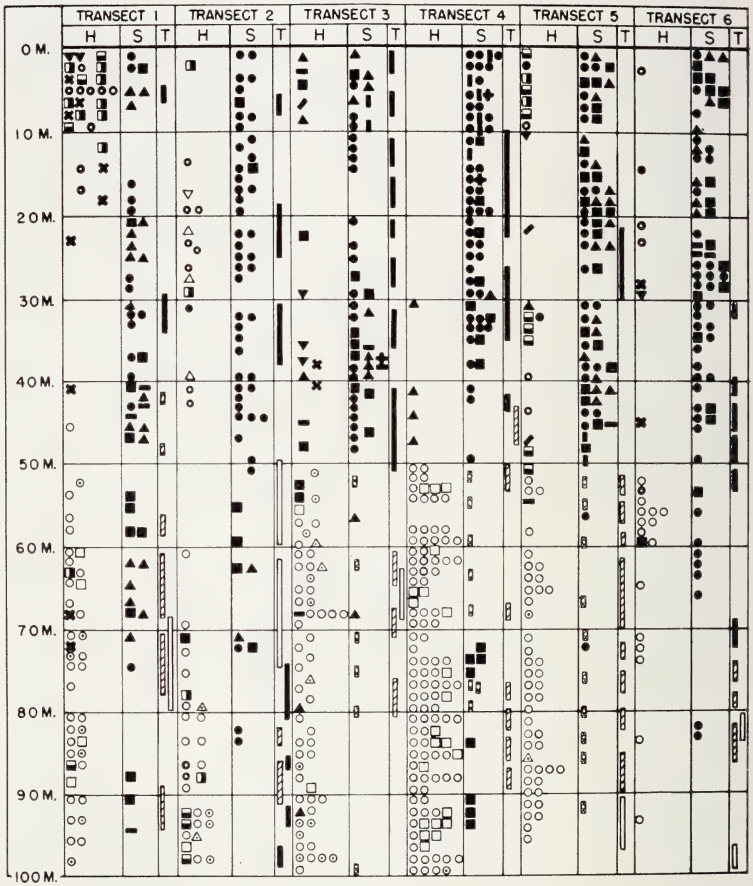

Fig. 1 Line transects through scrub (0-50m) and abutting sandhill vegetation (50-100m). Darker symbols represent typically scrub species.

nities. Those species most typical of the scrub are indicated by the darker symbols, those of the sandhills by the lighter ones.

The most obvious and important difference is in the herbaceous layer, especially the wire grasses *Aristida stricta* and *Sporopolus Junceus* (S. *gracilis* (Trin.) Merr). Only one small clump of *Aristida stricta* was on the scrub side, and 249 clumps of the combined species were on the sandhill side. While a much larger number of apparent clumps of wire grasses is shown in transect 4 than in any others, this may well be influenced by two factors. Shortly after a fire has burned off an area, the blades are too short to assume a horizontal position and are less apt to be intercepted, as was the case in transect 3. When fire has not occurred for many years, closely spaced clumps may be so enmeshed with both dead and living blades that they appear as a single clump. In transect 4 fire had been recent enough for the separate entities to be distinguished, but the blades were long enough to have spread horizontally and thus were more readily intercepted. The other four transects had not burned for at least 10 years, and their intercepts no doubt often coalesced to form compound clumps.

Woody species typical of the scrub such as myrtle and Chapman's oaks, *Lyonia ferruginea*, and sand pine are not infrequently encountered on the sandhill side but tend to become less common with increasing distance from the scrub. *Quercus chapmanii*, perhaps because of its thicker more fire resistant bark, tends to show proportionally greater survival in the sandhill side than does *Q. myrtifolia*. For example, on the scrub side 171 clumps of *Q. myrtifolia* occurred to 59 on the sandhill side. *Q. chapmanii* intercepts were 14 in the former and 16 in the latter.

The absence of fire permits a rapid invasion of the sandhills by sand pine where a seed source is available. This is best shown in transect 2. In transect 3 many 2-3 year old sand pines had been killed by the ground fire only a month previous to the sampling. This fire, incidentally, burned right up to the edge of the scrub where it apparently died out. Of the non-key species saw palmetto, *Serenoa repens*, was about equally distributed in each community (scrub side 27, sandhill side 35).

Soil Transects

Results from soil analyses were disappointing to me since I had long felt the sites of most scrubs are associated with marine features such as old dunes, bars, and beaches, where maximum washing and sorting of sands had occurred (Laessle, 1958a). However, except for five sites all on the "ridge" where the red, clayey "Citronelle" formation closely underlies the sandhill vegetation no significant soil difference between the soils of sandhill and scrub vegetation was apparent. Here, composite results are presented of comparisons from the two communities located near Kingsley Lake and Goldhead State Park in Clay County, Mogelvang's Scrub and the adjacent sandhill near Rock Springs in Seminole County, and the Clarcona area just southeast of Clarcona, Orange County. At these sites a very appreciable increase of phosphorus was encountered with increasing depth in the sandhill portions of the transects. The average extractable phosphorus in the scrub and sandhills, respectively, was as follows: 0-2 inch horizon, 4.97 vs. 14.32 ppm; 2-8 inch horizon, 1.35 vs. 25.08 ppm; 8-15 inch horizon, 0.92 vs. 26.97 ppm.

Samples from the two communities near Weekiwachee Springs in Hernando County, and at Inverness-Lecanto and near Citronelle in Citrus County, however showed average extractable phosphorus in the scrub and sandhills, respectively, as follows: 0-2 inch horizon, 4.54 vs. 5.05 ppm; 2-8 inch horizon, 3.32 vs. 2.23 ppm; 8-15 inch horizon, 2.30 vs. 1.32 ppm.

Neither the phosphorus nor mechanical analyses showed any overall consistent differences.

Slightly less yellow 8-15 inch samples from the scrub sides were often observed and may well be due to the higher amounts of organic acids leached from the greater accumulation of unburned litter encountered there.

Scrub unburned for 20 years or more had soil profiles with exchangeable cations of K, Ca, and Mg frequently 2-3 times higher than in the recently burned sandhills. For example, in the Citronelle transect the following analysis was obtained: averages from the pooling of the 3 horizons samples gave 28.8 ppm vs. 11.5 ppm for K, 290.0 ppm vs. 82.5 ppm for Ca, and 109.5 ppm vs. 36.25 ppm in scrub and sandhills, respectively. Garren (1943) stated that burning decreases the acidity, increases the Mg and replace-

able Ca and organic matter in long leaf pine soils, including that of the sandhills.

On the other hand, if both communities had been unburned for over 20 years such differences were negligible except for Ca and Mg which were twice as abundant on the sandhill side: K, 14.0 vs. 15.5 at 0-2 inch; Ca, 87.0 vs. 182.0 at 2-8 inch; Mg, 42.1 vs. 84.1 at 8-15 inch horizons.

Where appreciable difference in these elements is present in the upper horizon in the soils of the two communities it is doubtless due to the burning of the organic particles on the sandhill soils and their rapid loss through leaching. At the 8-15 inch horizon no consistent difference in these elements was evident.

Recent fires on the sandhill soils also tended to lower the C/N ratio and raise the pH. In general the scrub soils proved slightly more acid but comparisons between the soils in some transects such as the Mogelvant scrub and adjacent sandhill soils, neither of which had been burned for at least 20 years, show the reverse, even when run by the N-KCl method for the three horizons sampled. The pH was 4.5 vs. 3.6, 0-2 inch, 4.65 vs. 4.30, 2-8 inch, and 4.60 vs. 4.65, 8-15 inch with the scrub again first at each level.

DISCUSSION

With no substantiating evidence for any general chemical or physical differences in the soils of the two communities it has become necessary to reevaluate some of the ideas expressed many years ago. According to Webber, the nature and relations of the scrub associations cannot be discussed without comparison with the high pine association, as the two associations are so commonly found in juxtaposition and occupy so nearly the same types of soil in the same region and at the same altitude. He also mentions that the two communities may be at the same level or one uphill or downhill from the other. The change from one flora to the other is very abrupt between the tangled vegetation of the scrub and the open forest of long leaf pines with a ground cover mainly of grasses. The high pine lands burn over almost every year and this condition has probably existed for many centuries. The scrub association, however, is a fire-fighting machine.

Webber attributes the fire-fighting equipment to a number of

distinct factors. Nearly all scrub plants are evergreen and drop old leaves throughout the year. Scrub bushes and trees so fully occupy the soil that they absorb available moisture and nutrition to the extent that the flammable grasses and other herbs are excluded. The soil surface is thus relatively bare of flammable material except for gradually falling leaves and old twigs which rapidly rot and disappear. Furthermore, a natural fire break is maintained between the scrub and adjacent sandhill vegetation, as the extensive root systems of both communities probably limit the growth of flammable grasses and herbs between these communities.

Fire frequently approaches the scrub and dies out without gaining entrance. After a number of uninterrupted fire-free years, however, the scrub accumulates dead limbs and branches, and the fire-break margin becomes partially covered with grass. Under these conditions, a fire may ignite the scrub.

Webber's ideas of a natural firebreak between the two communities are often evident to the eye but are not obvious from the vegetational transects (Fig. 1), where the clumps of wire grasses and other more flammable herbs do not show an appreciable decrease in their numbers near the scrub border. If the size of the clumps of wire grasses is ignored there are in the six transects 41 such clumps within 10 m of the scrub borders, 50, 51, 56, and 52 in each successive 10 m interval from this boundary. But, individually, only transect 2 shows an obvious trend supporting this concept while in transect 6 the reverse is evident.

To Webber's explanation as to the occasional spreading of fire from the sandhills to the scrub, there should be added the fact that lightning-caused fires may arise in the scrub. The author has observed such an event when an old sand pine, heavily laden with Spanish moss, burst into flame when struck by a bolt of lightning. Old stands of sand pine are frequently festooned with dense growths of this epiphyte (Fig. 2) which is highly flammable when dry. Crown fires in the scrub could readily be started in this manner in only relatively dense stands of sand pine.

Spanish moss could also be an important factor in allowing creeping ground fires, which not infrequently gain access to the tops of sand pines and thus start crown fires in scrubs. I have observed many instances of multiple aged stands of sand pine

Fig. 2. A 50 year old stand of sand pine, 1/2 mile north of Cocoa City Limit on the E. side of U.S. 1, showing an abundant growth of Spanish Moss.

which no doubt developed after ground fires had partially opened scrubs by killing back much of the shrubby understory and even some of the sand pine. But, as mentioned by Webber, rapid sprout growth from the crowns of such burned scrub shrubs, soon develop enough shade to prevent the entrance of the heliotrophs from abutting sandhill vegetation, at the same time acting as nurse plants to any young sand pines started from seeds released by such fires. Cooper et al. (1959) showed that young sand pine seedlings cannot survive soil temperature above about 125 F.

Origin and Successional Relationships

Whitney likewise could find no apparent difference from chemical and physical analyses of the soils of these communities to account for their great vegetational differences and thought that it was chance that determined what area became scrub and sand-

hill associations and said that the two kinds of vegetation were not capable of growing together.

According to Webber, the origin of the large scrub areas is probably traceable in part to the poor, arid character of the soil on which the associated plants of the scrub can succeed better than any other group of plants. It would seem probable that in the early formative period of plant distribution in this part of Florida, the scrub oaks, because of their mode of spreading by sprouts from the roots and their adaptability to succeed in such arid soils, found in these areas an opportunity to dominate the other vegetation and finally to extend their territory as natural conditions permitted. This does not explain why scrub vegetation should become established instead of the sandhill type unless it can be proved that the scrub soils are actually poorer and drier than those occupied by sandhill vegetation.

I think it more than chance that scrubs for the most part occupy well drained positions on ancient marine shoreline features as dunes, bars, and beaches and even old fresh water shorelines and stream deposits (Laessle, 1958a). Even recent dunes are colonized by scrub species. It is relatively rare that scrubs cannot be tied to any of ancient marine or freshwater features. Yet some sandhill communities do occupy definitely dune topography, for example, the previously reported area east of Frostproof. This makes the problem difficult to deal with in a simple and satisfactory way. Evidence of greater tolerance of scrub species to salt spray is abundant. It is especially striking on the dunes just before entering St. Andrews State Park, Bay County, Florida (Fig. 3). No examples of the sandhill communities in such a severe environmental situation have been observed. The sites originally occupied by scrub vegetation fit most situations and the persistence of sandhill vegetation becomes more plausible in the light of the scrub's resistance to frequent fire as pointed out by Webber.

The present existence of scrub along the shoreline about Red Hill (see the Childs topographic Quadrangle, U. S. Geological Survey, 1953), mentioned by Laessle (1958a) as being mid-Pleistocene according to MacNeil (1950), is at least 1,000,000 years old and may be as much as 10,000,000, and thus Pliocene or even late Miocene (H. K. Brooks, 1966), a most striking example of

Fig. 3. A highly modified scrub on the second dune ridge 1/4 mile W. of St. Andrews State Park. This scrub not more than 150 yards from the Gulf of Mexico shows the effect of wind and salt spray. The sand pine though at least 60 years old scarcely reached 3 feet in height but had branches extending at least 25 feet to the leeward.

the scrub's persistence. Brooks further states that the maximum Pleistocene sea level did not exceed 90 feet above present and believes that the climate at many times in the Pliocene was as dry as that of Corpus Christi, Texas. Perhaps both the sandhill and scrub vegetation have existed and maintained their same positions without any great floristic change through all this time or even longer.

Possible successional relationships between the two communities have been most varied and speculative. The following from Garren summarizes some of the ideas concerning scrub forests at that time. According to Pessin scrub on dunes with no fire would be succeeded by long leaf pine, oak, hickory and on dunes with infrequent fire would be followed by long leaf pine. Harper (1940) thought that there would be no change with fire once in a lifetime. Webber thought that fire would destroy the scrub if frequent and it would be followed by turkey oak and bluejack oak. Albert thought that scrub fires in young, non-cone bearing pine

would be followed by scrub and myrtle oak, and that crown fires in older sand pine stands would result in no change.

To these ideas must be added those of Kurz who stated that high pine land vegetation was succeeded by scrub. Laessle (1942) considered that these communities had no seral relationship. Miller (1950) thought that sand pine scrub was succeeded by high pine-turkey oak. Laessle (1958a) stated: "Scrub and sandhill vegetation represent the two most prevalent well-drained sub- or fire-climax communities in peninsular Florida. Each in the absence of fire would eventually, and often very rapidly, be succeeded by predominately evergreen hardwood tree communities, known in much of the Southeast, as hammocks." Webber considered that even with the destruction of the high pine forest (sand hill community) scrub would very rarely replace it.

After extensive observation throughout most of Florida and southeastern Alabama, my thinking on the matter unfortunately cannot be summed up succinctly. Since the time when most of the above opinions were expressed many areas of sandhills which have close proximity to scrubs have been protected from fire for twenty or more years and the very rapid spread of sand pine from nearby scrub is very striking. One such area extends for many miles along U. S. 98 in the area included in the Eglin Air Force area, between Pensacola and Fort Walton. Here, with no sign of fire for a very long period, sand pines of all ages were present from 1.5 ft. d.b.h. to small seedlings but very little other typical scrub vegetation was present. Myrtle oak was sparse with scattered *Ceratiola* present. The other tree vegetation was predominantly sandhill species such as turkey oak and long leaf pine. Both wire grasses *Aristida stricta* and *Sporobolus junceus* were thin and scattered. Most of the other herbs were typical sandhill forms, the exception being *Rhynchospora dodecandra* which was frequent. The rapid spread of sand pines to the sandhill islands in the Ocala National Forest is nearly everywhere evident since fires have been prevented. Its spread in the sandhills at the University of Florida Conservation Reserve, Welaka, Putnam County, Florida, is continuing rapidly from a nearby scrub, since observed by Laessle (1958b). The same trend was also marked in the Camp Blanding area, particularly in the Clay County portion where at least two scrubs are known to occur.

The invasion of sandhills by the typically scrub oaks, *Q. myrtifolia* and *Q. chapmanii* is apparently much slower but their occurrence there with decreasing frequency as one moves further from adjacent scrubs is evident from the transects (Fig. 1). It would thus appear that the scrub species will differentially invade the sandhills but that a much longer fire free period must occur for complete replacement to be accomplished. It is also of interest to note that in spite of the supposed racial difference in the panhandle form and the peninsular form described by Little and Dorman (1952) in which the former was described as having less serotinous cones, seed release by both subspecies without fire is sufficient to cause their rapid invasion of adjacent sandhill communities when fire is eliminated.

Of interest in this regard is Webber's interpretation that the present limits of the large scrub areas became established centuries ago and that a state of near equilibrium has existed for many years. If Webber considers fires to be a natural condition in the sense that lightning frequently causes them in this region, then I agree with him but would extend the time of relative stability of the two communities to millions of years rather than hundreds.

The Florida scrub is the ecological equivalent of the California chaparral and according to Axelrod (1958) extensive paleobotanical studies over the past 40 years have shown that chaparral has been a major plant formation in California since mid-Pliocene.

The fate of scrub kept fire-free for extended periods of time is not as clear as I once thought (Laessle, 1942, 1958a). One scrub on Bear Point, an arm like projection into Lake Placid's eastern shore, just north of Childs, Highlands Country, Florida, has been protected from fire for an extended period and is composed of typical scrub flora except for a complete lack of sand pine. This scrub has the aspect of a hammock but lacks any characteristic arboreal hammock species. Part of this peculiarity may be the lack of a seed source in this region of such typically hammock species such as *Magnolia grandiflora, Quercus laurifolia, Carya glabra, Ilex opaca, Persea borbonia, Cornus florida,* etc., which are rare and far from this site. Such typical scrub species as *Carya floridana* with a d.b.h 13.1 inch and *Quercus myrtifolia* with a d.b.h. of 11.0 inch were observed as also were such characteristic hammock species as *Mitchella repens* and *Callicarpa americana.*

Though no signs of fire were detected on the tree trunks here, charcoal was detected in a soil sample at a depth of 7-8 inches. The nearest sand pines were at least a mile from this scrub.

It seems very likely that sand pine formerly occurred here but the lack of fire for an extended period has not permitted its regeneration. Sand pines over 75 years old are very rare and on this basis a fire free period of at least this duration is suggested.

Another very old scrub with a few large and widely scattered 72 year old sand pines was studied on U.S. 1, about 1 mile south of the Rosedale Road, Indian River County, Florida. Though no sign of fire was observed on the oldest trees, charcoal was also abundant in the soil here. There were a few 8-10 foot sand pines and a few small seedlings but the ground vegetation was very sparse consisting mostly of lichens with extensive areas of bare white sand. Lichens, *Cladonia evansii*, *C. leporina*, *C. subtenuis*, and *C. prostrata* comprised 11.9 per cent of the ground cover. The per cent of shrub cover, mostly *Ceratiola ericoides*, *Quercus myrtifolia*, and *Serenoa repens* was only 15.6 per cent. The tree canopy composed almost exclusively of sand pine was only 23.19 per cent. It is difficult to imagine how this sparse vegetation could possibly support a fire either of ground or crown type which could initiate a rejuvenation of the scrub vegetation. No signs of any invasion of hammock species were observed. It thus appears that it is possible for scrubs to run out, or at least, reach a very depauperate condition in which state they may remain indefinitely.

A similar and almost as sparsely vegetated scrub was studied at Destin, Okaloosa County, Florida. Here no fire was evident on the bark of sand pines, some of which were over 105 years old. Ground vegetation composed only 9.9 per cent cover which was mostly *Cladonia evansii*, *C. subtenuis*, *C. leporina*, and *Dicranum condensatum*. Shrubs formed 33.8 per cent cover largely of *Quercus myrtifolia* and *Chrysobalanus oblongifolius*. The tree canopy was 40.1 per cent, 33.36 of it being scattered sand pine which in spots contained some juvenile trees. No signs of invading hammock species nor species typical of any other community were detected. Here charcoal was also found in the soil. Parts of this scrub contained enough sand pine reproduction and ground vege-

tation to make rejuvenation possible either by means of ground or crown fire, but this scrub's fate seems dubious.

It is worth noting that the three scrubs described above are small and isolated from abutting sandhill vegetation or any other flammable communities.

On the other hand scrubs showing evidence of succession toward hammock are not infrequently encountered. One such example was studied on the offshore bar and dune system just West of U.S. A1A, about a mile north of Ormond Beach, Volusia County, Florida. Here fire protection has been in effect for a considerable period due to its close proximity to many dwellings. Many laurel oaks, red bays, and a few *Magnolia grandiflora* were thoroughly mixed with scrub species. Although the sand pines were quite mature, many in the 8-10 inch d.b.h. class, the larger laurel oaks were only about 2 inch d.b.h. Soil analysis in the exchangeable cations, K, Ca, Mg, and P while higher than in most scrubs studied were not appreciably different from others which showed no signs of invasion by hammock species. Young scrub soils, as the one here, may not have been subject to the leaching of elements for a long period as were many of the very old inland ones and this factor may well be of significance.

I have observed no evidence of succession toward sandhill vegetation from scrub. There are, however, some typically sandhill plants as *Quercus laevis* found in extensive otherwise typically scrub areas, notably in many portions of the Ocala National Forest. Here they are always scattered and not generally accompanied by any appreciable number of young trees. Here, also, are occasional sandhill herbs such as *Stillingia spathulata* and stinging neetle, *Cnidoscolus stimulosus* but never in large numbers and only when a more clayey subsoil is found within a foot or two from the surface or when there is evidence of mixture of dune sand with soils from nearby areas supporting sandhill vegetation, (Laessle, 1958a). I have never observed the invasion of *Pinus palustris* in the scrub. This supports the observations of Webber that large long leaf pine trees extend entirely to the margin [of the scrub]. The complete absence of the remains of the extremely decay-resistant heart of longleaf stumps even in the periphery of the scrub was given by Laessle (1958a) as supporting evidence of the past spatial stability of the two communities.

However, the finding of sandhill vegetation on definitely dune topography as a shoreline feature of the Sangamon interglacial stage as reported by the author (1958a, p. 375), does hint at the idea that scrub vegetation may have formerly existed there and that an unusually high frequence of fire may have eliminated it.

Conclusion

Webber's paper was based on his observations on inland scrubs, many of which lack the higher phosphorus content observed in abutting sandhills. He believes the lack of frequent fires in the scrub, and their almost yearly occurrence in the sandhills, to be the most important single factor responsible for the maintainence of the very sharp boundary between the communities and to account for their spatial stability for the very extended periods.

Where scrub is not isolated from higher sandhill vegetation the former occupies the more coastal position probably because of the greater salt spray tolerance of scrub vegetation, the factor that ground fires burn down hill with difficulty, and the fact that on-shore winds would tend to keep fires less frequent in the areas occupied by scrub. In the light of well established Cenozoic shorelines away from present coastlines, similar origins for most of the more ancient scrubs is postulated.

There remains the problem of explaining the scrubs which cannot be tied to the definitely ancient shore lines. Part of this difficulty may be due to the great changes in topography that have been wrought by the karst nature of Florida which has extensively changed the original topography through solution of the soft Ocala limestone. Furthermore, many of such problematic scrubs are partially or completely bordered by vegetation much less subject to frequent fires than in the sandhills. Provided the soil is poor and excessively drained, even subtle differences in fire frequency may be enough to permit the development of such partially fire-protected scrubs.

While scrubs are remarkably similar with regard to their major vegetative components their apparent isolation from each other is not as great as one might at first believe. Such important scrub elements as myrtle oak (*Quercus myrtifolia*), Chapman's oak (*Q. chapmanii*), live oak (*Q. virginiana*, with its many variations),

and tree lyonia (*Lyonia ferruginea*) frequently occur in the drier portions of intervening "scrubby flatwoods" of Laessle (1942). These species also are often widely scattered in the sandhills and drier hammocks. The major gap in the range of typical scrubs containing sand pine is between the inland peninsular scrubs in Clay County and the panhandle scrubs the nearest of which are in Franklin County, a distance of approximately 150 miles. The nearest coastal peninsular scrub at Cedar Key, is over a hundred air line miles from the Franklin County scrub. If the range of sand pine were once more continuous, it is most likely that very considerable erosion of the limestone plain in the region of the Suwannee River Valley is the most plausable cause for the large gap in the present range of the sand pine (H. K. Brooks, personal communication). If the separation of sand pine into two races, a panhandle form and a peninsular form is valid, as proposed by Little and Dorman, this gap in the present range must have existed for a considerable period.

The present sandhill vegetation presents no such spatial problem, as this community is nearly continuous from at least south central North Carolina, and Hale County in central Alabama, to its southern limit in Desoto and Highlands counties, Florida.

In conclusion, there is little doubt that these most distinct communities have existed essentially unchanged, for the most part from at least the Miocene, and that the differential frequency of fire in them has played the major role in maintaining their most contrasting floristic and structural characteristics. Soil difference between scrub and sandhill areas, at least as far as the macro-elements and physical characteristics present are concerned, are not consistently great enough to account either for the generally sharp boundary between them, nor for their more general spatial pattern.

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